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Species distribution modelling tools and databases to assist managing forests under climate change

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ABSTRACT

This paper examines progress made with species distribution modelling (SDM) for trees under climate change. Following brief background information, the main focus is on developments in the last five years. Correlative SDMs have become the most commonly used approach for analysing potential climate change impacts on areas suitable for particular species. The use of SDMs has been criticized, but responses to these criticisms are provided and limitations may not be as great as has been suggested. For many species SDMs are the only potential source of data for learning about likely climate change impacts, and suitable occurrence data for SDM analyses exist for about 50 000 tree species. SDM papers have already been published presenting analyses for more than 1000 tree species under projected climate change. Most SDM climate change analyses adopt an 'equilibrium assumption' that tree species natural distributions provide a reliable estimate of their climatic requirements. However, in addition to natural distribution data, data from trials outside their natural distributions are desirable to determine their intrinsic climatic adaptability. Progress is described in relation to climatic data, soil data, species distribution data, species and provenance trial data, descriptions of species climatic requirements, mapping of suitable areas and integration of species and environmental data. Desirable future objectives are identified for each of these topics.

1. Introduction

Managing trees under climate change is a great challenge for forestry in the present century (Millar et al., 2007). It will involve adjustments in ecological, social and economic systems (Spittlehouse and Stewart, 2003). These changes will need to be evidence-based and underpinned by appropriate models and data. Immense progress has been made in developing tools and databases to support forestry decision-making under climate change, but major challenges remain.

The aim of this review is to provide an overview of some of the key recent advances relevant to determining where particular tree species may be able to grow in either natural forests or plantations under current and future climatic conditions. The focus is mainly, but by no means entirely, on species of the genus *Eucalyptus* as they have advantages for climate change studies. For example, eucalypts have very poor dispersal capabilities (Booth, 2017a), so the survival of existing stands is the key issue for the present century. The great complications of assessing possible dispersal to and establishment at other sites are avoided. Eucalypt species and provenances have also been extensively tested outside their natural distributions, so knowledge of their climatic adaptability beyond their natural distributions is good at least for the commercially important species (Jacobs, 1981, Booth et al., 2015).

There has been a great increase in species distribution modelling (SDM) since the first package called BIOCLIM became available in 1984 (Nix, 1986; Booth et al., 2014). For example, Dyderski et al. (2018) identified 124 papers from the Web of Science published between 1996 and early 2017 that analysed more than 500 tree species distributions and produced projections based on at least one climate change scenario. Most of these papers focussed on threatened, invasive or plantation species. The contents of these papers, including abstracts and ten important features, were summarised in an Excel spreadsheet available as an appendix to the Dyderski et al. (2018) paper. For example, the geographic spread of the studies was as follows: Global (2), Africa (8), Asia (36), Australia (4), Europe (32), North America (38) and South America (4). Though widely used the SDM approach is not without some limitations for examining how tree species will respond to climate change (Keenan, 2015). However, these limitations may be less for eucalypt species than many other tree species (see Table 1).

If they are available the use of more detailed process-based models may be desirable for studying climate change impacts. But presently their applications are confined to a very small number of relatively well-known species of commercial importance (see, for example, the climate change analyses of *E. globulus* and *E. nitens* plantations by Battaglia et al., 2009; Battaglia and Bruce, 2017). In contrast, three

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Table 1
Limitations of species distribution models (SDMs) for predicting the impacts of climate change on forests identified by Keenan (2015) and responses particularly relevant to eucalypts.

Challenge	Response
• Predicting capacity of species to move	• Eucalypts have very poor dispersal capabilities, therefore the key issue is whether they will survive where they are currently located (see Booth, 2017a)
• Local adaptation (refugia)	• Trials can indicate climatic adaptability of provenances (Eldridge et al., 1993), but there is a need for higher resolution data to detect refugia (Austin and Van Niel, 2011)
• Uncertainty in predicting future climate	• A challenge for all models. Some uncertainty is inevitable until specific global mitigation actions are agreed and enforced
• Predicting and incorporating effects of extreme events on tree populations	• See, for example, Yan Hong (2001) 'Frost prediction for Australian tree species in China'. Absolute (i.e. record) minimum temperature is an appropriate estimate for use in SDMs
• Lag effects and gene flow within species -species still responding to past changes	• Eucalypt species and provenance trials can provide insights (Booth et al., 1988, Booth, 2017b). Genomic studies are providing useful information (Supple et al., 2018)
• Epigenetic effects i.e. growing conditions influencing ability of progeny to cope with drier or warmer conditions	• More research is needed, but progeny trials outside natural distributions (Eldridge et al., 1993) could provide some insights
• Biotic effects (diseases and insect pests)	• Can be modelled using SDM or more complex models (see, for example, Berthon et al., 2018 rust paper using Maxent SDM)
• Phenology and life history traits	• Overseas trials provide insights e.g. poor flowering of *E. nitens* in South Africa (Germishuizen and Gardner, 2015)
• Mutual benefits with other plants or animals that may respond differently to climate	• Unlikely to be critically important if trees are already well established at particular sites
• Competition effects	• Not very important when considering vulnerability of established stands. Competition is mainly during establishment

SDM studies have examined the likely impacts of climate change on many *Eucalyptus* and closely related *Corymbia* species (which were previously classified as eucalypt species). These studies considered the likely impacts on 819 species (Hughes et al., 1996), 108 species (Butt et al., 2013) and 657 species (González-Orozco et al., 2016). The Hughes et al. (1996) paper did not project future distributions using a climate change scenario, so it was not listed by Dyderski et al. (2018), though the Butt et al. (2013) paper was listed. The González-Orozco et al. (2016) analysis projected future distributions and fell within their assessment period, but was missed by Dyderski et al. (2018). Including this analysis would have increased the number of tree species distributions assessed under climate change to over 1000. There are no other broad-scale analyses of the likely impacts of climate change on most eucalypt species using alternative approaches. Accordingly, as SDMs are the only source of climate change impact information for many eucalypt and other tree species it is worthwhile to recognize their limitations, but also to consider how they may provide useful information.

In the latest SDM study of eucalypt distributions González-Orozco et al. (2016) made it clear that they were aware of concerns about the 'equilibrium assumption'. This implies that analysis of just the current natural distribution provides a reliable indication of a species climatic requirements under climate change. Various authors have pointed out the need to analyse not only the natural distribution, but also occurrences outside the natural distribution (see Booth, 2017b for a review of the 'equilibrium assumption'). González-Orozco et al. (2016) attempted to address the issue by using models which avoid 'over-fitting' (see Booth, 2017c for a discussion of some of the limitations of the González-Orozco et al., 2016 analysis and how they might be overcome). Despite some limitations the paper provides much useful information, including maps of projected responses for the 657 species as part of the supplementary information. An advantage of the approach is that it can be applied to large numbers of species. A disadvantage, in comparison to use of data from both the natural distribution (i.e. realized niche *sensu* Hutchinson, 1957) and trials outside the natural distributions (c.f. fundamental niche *sensu* Hutchinson, 1957), is that it assumes all variables have climatic adaptability beyond the realized niche. The analyses in Booth et al. (1988) suggest that this is not the case, but more work is needed examining species climatic responses in locations outside their natural distributions.

The requirements for using SDM techniques to deliver "a global climatological audit to assist conservation and sustainable development" in forests under climate change were outlined by Booth (1991). The paper identified five key objectives related to climatic data, species distribution data, species and provenance trial data, descriptions of species climatic requirements and mapping of climatically suitable areas. These topics are used here as section headings. Within each section, progress is described and then desirable future objectives are outlined. An extra section has been added after climatic data to consider soil data. The biodiversity database known as the Atlas of Living Australia (ALA) has integrated elements of the five key objectives into one unified system freely available on the internet (spatial.ala.org.au) and this is described in a separate section.

2. Topic areas

2.1. Climatic data

The outstanding achievement in relation to global climatic data has been the development of the WorldClim database (Hijmans et al., 2005). This has recently been updated with WorldClim 2 (Fick and Hijmans, 2017) providing improved climatic databases for land areas of the world. These were developed by applying thin plate spline methods (Hutchinson, 1991, 2013), which were originally used to prepare Australian interpolation surfaces for the BIOCLIM package. The WorldClim 2 website (worldclim.org/version2) provides access to average monthly data for minimum, mean and maximum temperatures as well as precipitation. The 19 bioclimatic variables originally created for BIOCLIM are also available. Climate change scenario data for four representative concentration pathways (RCPs) used in the Fifth Assessment of the Intergovernmental Panel on Climate Change (IPCC, 2014) are available at the original WorldClim site (worldclim.org). Both the WorldClim and WorldClim 2 data are available at resolutions down to 30 s (i.e. 0.5 min or about 1 km^2). The fact that the Hijmans et al. (2005) paper has been cited more than 13 000 times in the Google Scholar reflects its general dominance in this area. However, other climatic databases including CliMond (Kriticos et al., 2012), CHELSA (Karger et al., 2017), MERRAClim (Vega et al., 2017) and ENVIREM (Title and Bemmels, 2018) have been developed for specialised needs.

2.2. Climatic data – Desirable future developments

The BIOCLIM package as launched in 1984 (Nix, 1986, Booth et al., 2014) included interpolation relationships and estimated climatic

conditions for the actual locations of occurrence. In contrast, most current SDM analyses take their estimates from the nearest point in interpolated grids, usually from WorldClim. For instance, Dyderski et al. (2018) provide grid resolutions ranging from 20 km to 25 m for all but five of the 124 papers, with the approximately 1 km^2 resolution of WorldClim being the most commonly used (61 papers).

Interpolating to actual locations would allow the use of more sophisticated approaches analysing local topography and hence would provide improved estimation of microclimate effects on important factors such as insolation (Sabetraftar et al., 2010) and frost (Bramer et al., 2018). This would help to locate potential refugia with different microclimates to surrounding areas. Austin and Van Niel (2011) provide a simplified example, including some limited topographic data (i.e. position on slope) as well as climatic information, for an analysis of the natural distribution of *Eucalyptus fastigata*.

2.3. Soil data

As the key issue for eucalypt species under climate change is survival at existing sites (Booth, 2017a), data on soil conditions are not essential. However, soil data will be important for many tree species that have more effective forms of seed dispersal.

Availability of global soil data has lagged behind that of global climatic data, as standard data for sample points are not so readily available and discontinuities in soil types mean the challenges for interpolation are greater. However, significant progress has recently been made with the release of the SoilGrids250m database by a group led by the International Soil Reference and Information Centre (ISRIC) (github.com/ISRICWorldSoil/SoilGrids250m, Hengl et al., 2017a). This provides global predictions for standard numeric soil properties (organic carbon, bulk density, Cation Exchange Capacity (CEC), pH, soil texture fractions and coarse fragments) at seven standard depths (0, 5, 15, 30, 60, 100 and 200 cm), in addition to predictions of depth to bedrock and distribution of soil classes based on the World Reference Base (WRB) and USDA classification systems (ca. 280 raster layers in total). Accuracy assessment of both numeric and categorical variables was based on a 10-fold repeated cross-validation. Each model was refitted 10 times using 90% of the data and comparing fitted models with the remaining 10% of the data. The models explained between 56% (coarse fragments) and 83% (pH) of variation in the data with an overall average of 61%. While these values are not high they are already providing some useful data for analyses of climate change impacts on tree species as described below.

Interestingly, recent advances in interpolation of soils data have been possible because of the use of non-linear interpolation methods similar to some of those used in climatic interpolation (see Guisan et al., 2017 for explanations of different methods). The ISRIC group have also shown how important variables for plant growth, such as rootable depth and plant-available water holding capacity, can be derived using the SoilGrids250m and other data (Leenaars et al., 2018).

Further research is needed to provide global interpolated estimates for soil chemical factors, including major plant nutrients such as nitrogen, phosphorus and potassium for the whole world. However, the same ISRIC group responsible for the SoilGrids250m data has already developed interpolated soil nutrient relationships at 250 m for sub-Saharan Africa (Hengl et al., 2017b). Predictions were produced for organic carbon, the six macronutrients and seven micronutrients.

Although the SoilGrids250m data have only become available recently they have already been used in two climate change study of trees. Lyam et al. (2018) used the data to examine the impact of climate change on the distribution of *Senegalia senegal* in West Africa. The Maxent (maximum entropy) SDM (Phillips et al., 2006) indicated the current distribution to be strongly related to extractable nitrogen, coarse fragments and soil organic carbon stock, as well as precipitation of the warmest and coldest quarters and mean temperature of the driest quarter.

Manchego et al. (2017) have also used Maxent to study distributions of 17 tree species in southwestern Ecuador. From 22 climatic and soil predictor variables they found annual mean temperature, mean diurnal range, precipitation seasonality, wettest quarter precipitation, driest quarter precipitation, soil classification (USDA), soil depth (absolute depth to bedrock) and soil organic content (fine earth fraction) were biologically meaningful.

2.4. Soil data – Desirable future developments

Interpolating soil data to occurrence locations would, like climatic interpolation, allow the use of more sophisticated approaches using local topography. Analysing data from nearest grid points, as well as factors such as length of slope and position on slope to estimate soil depth, would allow water holding capacity to be estimated for occurrence locations. This would help to locate potential refugia with different environmental conditions to surrounding areas.

2.5. Species distribution data

The development of biodiversity databases has made species distribution data readily available. More than 910 000 records of natural occurrences of eucalypt species are available from the Atlas of Living Australia (ALA, Belbin, 2011, ala.org.au). Data for other tree species natural distributions are available from the Global Biodiversity Information Facility (GBIF, Hobern et al., 2012, www.gbif.org).

Some caution is necessary in using data from biodiversity databases in SDM analyses (Gomes et al., 2018). Heap (2016) and Serra-Diaz et al. (2017) have described how to screen tree species distribution data before their use in SDMs. This involves the removal of non-spatially located occurrences, as well as duplicate locations and other types of spurious observations. Serra-Diaz et al. (2017) aggregated data from five sources including the GBIF. They analysed 36.69 M occurrence records for 49 206 tree species and found only 6.40 M to be high quality records suitable for SDM analysis. However, 63% of records were rejected because they were additional records within the approximately 1 km^2 grid cells used i.e. only one observation was accepted from each cell.

2.6. Species distribution data – Desirable future developments

Currently both the GBIF and ALA provide occurrence data only as presence at specific dates, not absence. Reliably verifying absences poses much greater problems than recording presences, particularly for small or highly mobile species. In contrast, tree species are relatively easy to record as confirmed absences within defined areas, so they would be suitable for pilot GBIF or ALA projects providing absence as well as presence data. Information on changing distributions over time, particularly local extinctions, is obviously important for analysing the ongoing impacts of climate change.

2.7. Species and provenance trial data

Most species elimination and provenance trials are aimed at identifying taxa with commercial potential (Eldridge et al., 1993). Once the most promising taxa have been identified the relative failures are of no commercial interest. For example, more than 200 eucalypt species were assessed for introduction into China (Turnbull, 2007), but plantations are now dominated by clones of the hybrid *Eucalyptus urophylla* x *E. grandis*, with smaller areas of *E. camaldulensis*, *E. dunnii*, *E. globulus*, *E. maidenii*, *E. pellita*, *E. saligna*, *E. smithii* and *E. tereticornis* as well as hybrids of some of these species (Xie et al., 2017).

Published reports of species elimination and provenance trials in scientific journals have tended to concentrate on describing the performance of promising taxa. Information on where less promising taxa have failed to thrive or have died would be useful in helping to

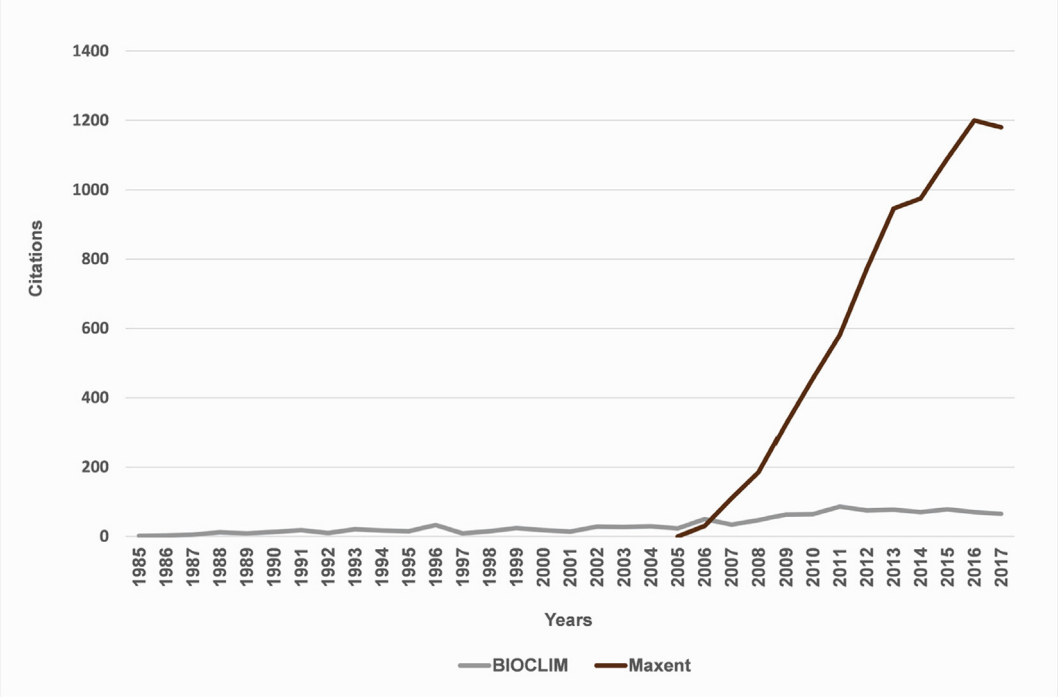

Fig. 1. BIOCLIM and Maxent citations in Google Scholar. Citations are based searches on the words 'BIOCLIM' and 'Busby' before 1991 and then the Busby (1991) paper, while citations of the Phillips et al. (2006) paper are used for Maxent. The Busby (1991) and Phillips et al. (2006) papers have been cited more than 1000 and more than 8600 times respectively.

understand how their natural populations might respond under climate change. However, details of failures, and particularly likely reasons for failures, are usually confined to unpublished reports. There are relatively few examples of publications summarizing all the major species trials within a region. The book by Poynton (1979) describing trials of 88 eucalypt species at 271 sites in southern Africa is a notable exception. As the major wave of eucalypt species introduction and provenance trials took place during the 20th century (Jacobs, 1981, Eldridge et al., 1993) many of the unpublished results have now been lost.

Though detailed data from trials are not available from the Global Biodiversity Information Facility (GBIF, Hobern et al., 2012, www.gbif.org) it currently holds more than 930 000 occurrence records for the genus *Eucalyptus*. These are mostly natural distribution records from Australia provided by the ALA, but about 56 000 are occurrences outside the natural distributions. These relate mainly to species of commercial importance and coverage is poor in some areas such as India and South-East Asia, but may be useful for some analyses.

Occurrences outside natural distributions may be introductions, naturalizations or invasions. Hui et al. (2014) found that of 373 eucalypt species introduced outside their native range, 82 have become naturalized and eight are invasive. Following introduction (either intentionally for trials or accidentally) naturalization may occur when a species spreads and barriers to reproduction are overcome. Some species may become 'invasive' if they spread more effectively and become weeds. Richardson et al. (2000) defined this as being able to spread more than 100 m in less than 50 years by dispersing seed or other propagules. This is towards the limit of usual spread rates for eucalypts (Booth, 2017a). However, *Eucalyptus camaldulensis*, unwisely planted along river banks in southern Africa, has spread many kilometres by seed floating down rivers and colonising new areas.

In terms of determining species climatic adaptability, data from trial introductions are probably most valuable as unimproved seed of known origin are usually grown under conditions where competition with other species is minimised. Naturalized observations may also be useful, but are growing in competition with often unknown local species and they represent a fraction of the species for which data is potentially available from trials. Invasive observations may also be useful, but represent an even smaller fraction of species tested in trials. The desirability of considering information from trials, if available, is illustrated by considering eucalypt species tested in southern Africa (Poynton, 1979). Of the 88 species evaluated in trials only 28 currently have southern African occurrences available from GBIF.

2.8. Species and provenance trial data – desirable future developments

Data collected from trials of species and provenances outside their natural distributions are of great value in assisting tree introductions, as well as predicting how natural and plantation stands may respond under climate change. A tree crop database called TREDAT was developed in Australia (Brown et al., 1989). This included sections for site description, management history, performance record, botanical identity and project description. Data for 921 taxa, 558 sites and 4375 performance records were collated, but unfortunately the system is no longer available and with changing computer storage systems the data have been lost. The revival of a database such as TREDAT would provide valuable information for climate change studies, but at present it is difficult to see an organisation that would fund such a venture.

It would be useful for climate change analyses if just locational data were readily available for plantations of particular tree species across the globe. Such data are often held by national or international agencies, but publicly accessible data are usually aggregated into broad types, such as softwood and hardwood (see, for example, the map available at http://www.agriculture.gov.au/abares/forestsaustralia/Documents/npi_regions_24_02_2014.pdf) or broad regions (see, for example, FAO, 2006) which makes them of little or no value for climate change analyses.

2.9. Descriptions of species climatic requirements

The pioneering SDM studies from 1984 to 1991 have been described by Booth et al. (2014) and more recent advances in analysing the climatic requirements of species or other taxa have been described in

three books (Franklin, 2009, Peterson et al., 2011, Guisan et al., 2017). There are many SDM methods available, but studies across all application areas have been dominated by the use of the BIOCLIM package in terms of longevity (Nix, 1986, Busby, 1991, Booth et al., 2014) and by the Maxent package in terms of numbers of recent applications (Phillips et al., 2006) (see Fig. 1). Some of the advantages and disadvantages of these methods have been discussed by Booth (2018). The first SDM climate change studies using BIOCLIM were published in 1988, but are not described in any of the three books. This is unfortunate as one involves native forests and the other plantations, and both are relevant to the 'equilibrium assumption' (see Booth, 2018).

While the pioneering BIOCLIM package describes species requirements in terms of variable ranges (or percentile ranges), Maxent provides response curves for variables. Comparisons between BIOCLIM and Maxent have often been skewed in favour of Maxent by the use of relatively few variables. There is little improvement in Maxent analyses when more than about nine variables are used (see, for example, the papers by Manchego et al. (2017) and Lyam et al. (2018) mentioned in Section 2.3.1 and Fig. 5 in Navarro-Cerrillo et al. (2011) which shows the effects of adding variables one-by-one). BIOCLIM can produce quite similar results to Maxent for both current and future climatic conditions when an appropriately large number of variables are used. For example, Penman et al. (2010) used the 35 variables recommended for use in BIOCLIM since 1999 and produced maps using both BIOCLIM and Maxent for current climatic conditions as well as three climate change scenarios. These were remarkably similar for the two methods, with BIOCLIM producing "good" results while Maxent produced "excellent" results.

Describing species distributions in terms of response curves for a few variables is an important advantage of Maxent and the uptake of Maxent was encouraged by comparative studies such as that of Elith et al. (2006). Maxent also appeared at a time when global climatic data became available and there was greatly increased interest in climate change studies, so these factors all account for some of the remarkable rise shown in Fig. 1. However, it is not widely appreciated how much Maxent applications have built on BIOCLIM developments with most terrestrial Maxent studies using the set of 19 BIOCLIM variables and global climatic data estimated using interpolation routines prepared originally for BIOCLIM (see Booth et al., 2014, Booth, 2018).

Of particular interest here are the 124 SDM papers relevant to tree species and climate change described by Dyderski et al. (2018) with *Fagus sylvatica*, *Pinus sylvestris, Quercus robur, Acer saccharum* and *Populus tremuloides* each appearing in 10 or more separate studies. A graph of SDM forestry climate change studies by year of publication is provided by Booth (2018). Only 12 of the 124 papers used process-based models such as PHENOFIT (Chuine and Beaubein, 2001), CLIMEX (Sutherst and Maywald, 1985) or 3-PG (Landsberg and Waring, 1997). The vast majority used correlative SDM approaches based on envelope and distance, regression, classification, boosting/bagging or maximum entropy methods (see Guisan et al., 2017 for descriptions of these methods and scripts in the R programming language to implement them). The Maxent model (Phillips et al., 2006) was by far the most common method applied. It was used in 32 studies of the 124 studies, with 10 applications accounting for half the papers published in the last complete year assessed (2016).

2.10. Descriptions of species climatic requirements – desirable future developments

The limitations of the 'equilibrium assumption' should be recognised for long-lived tree species. Almost all the 124 climate change studies described by Dyderski et al. (2018) are based on the 'equilibrium assumption'. That is they assume that analysis of a species current natural distribution provides a reliable estimate of its climatic requirements under climate change.

Competitive processes for trees in natural stands are most intense during establishment. Once established, many trees may occupy a site for many decades. Under climate change it is reasonable to assume that they may display some of the climatic adaptability they demonstrate when grown in trials outside their natural distributions. Results from trials outside species natural distributions suggest that it would be dubious to assume a tree of a particular species will inevitably die if it experiences conditions different to those of its current natural distribution (see Booth, 2017b for more on this issue).

2.11. Mapping of suitable areas

The development of geographic information systems and particularly free access via the internet to sophisticated tools such as the ALA has made computer mapping of climatically suitable areas readily available.

2.12. Mapping of suitable areas – desirable future developments

It would be desirable to see all users have access to systems as sophisticated as the ALA for their relevant regions and access to even higher resolution data.

2.13. Integrating species and environmental data – The Atlas of Living Australia (ALA)

The spatial portal of the ALA (Belbin, 2011) provides ready access to four of the five objectives identified in the Booth (1991) paper, and data on the location of successful trials, introductions or invasions can be easily imported into the system (see Fig. 2). Interpolated data across Australia are available within the ALA for more than 500 environmental, social and political variables, including the 19 BIOCLIM bioclimatic variables. Global data are also available within the ALA for the 19 BIOCLIM variables provided by WorldClim (Hijmans et al., 2005). Data stored within the ALA on species distributions can be readily loaded in the spatial portal (spatial.ala.org.au, add to map/species). Descriptions of species climatic requirements can be developed by analysing distributional data using scatterplots (tools/scatterplot) and more sophisticated tools such as envelopes, which are somewhat similar to BIOCLIM (add area/define environmental envelope) and even Maxent models (tools/predict). Computer mapping of suitable areas is readily available (see Booth, 2014 for an explanation of how to use these ALA tools along with data from the GBIF).

A particularly useful feature of the ALA (only available when using the freely available Chrome™ internet browser) is the ability to click on an occurrence location and bring up detailed information. This includes information on who recorded the observation, when the record was made and how accurately it is located. The results of more than 25 data quality tests are listed, including identification of suspected outliers. Details are also provided for more than 50 environmental variables.

Prober et al. (2015) have proposed the use of 'climate-adjusted provenancing' for forest restoration projects. This involves using seed taken from areas that currently experience climatic conditions similar to those expected in the future at a target restoration site, as well as locally sourced seed. The ALA and 'Climate Change in Australia' websites (www.climatechangeinaustralia.gov.au) can be used to identify suitable areas. With the help of Google Earth images shown at the highest mapping resolution available in the ALA, individual trees potentially suitable for sampling can be identified (Booth, 2016). Genomic studies have the potential to assist with this process (Supple et al., 2018), though these should become even more useful when measures of genetic similarity are based on climatically important genes.

The ALA includes a limited number of climate change surfaces. However, due to the number of different scenarios and potential future dates that could be used including them all as surfaces within the ALA is not practical. Accordingly, for more sophisticated climatic change analyses the ALA provides links to download distribution data to the

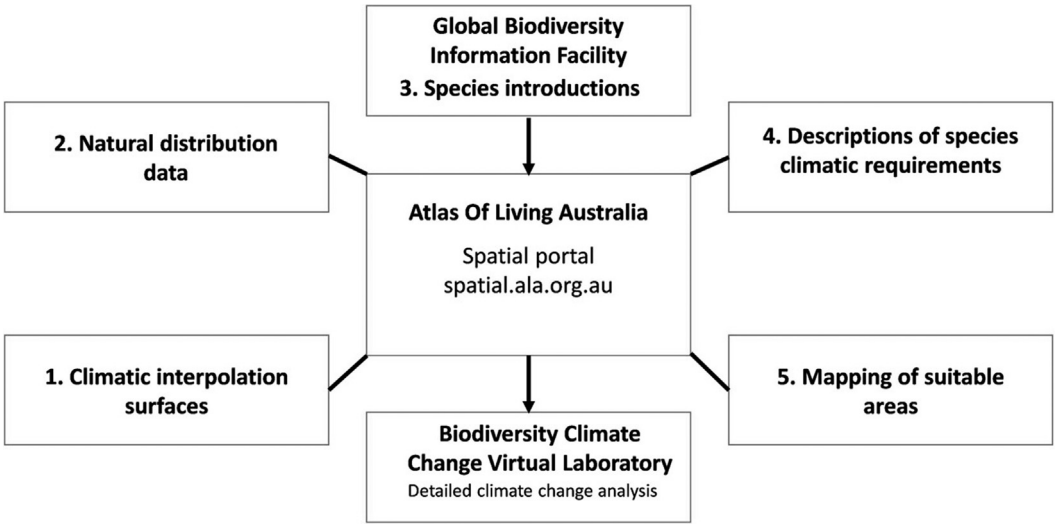

Fig. 2. The ALA, GBIF and BCCVL provide a powerful set of complementary resources for species climate change studies.

Biodiversity Climate Change Virtual Laboratory (BCCVL) (Hallgren et al., 2016).

Though the ALA does not provide access to data from tree species or provenance trials it does provide functionality to load data into the system for analysis. This might include data from tree species introductions obtained from GBIF or data on pests or diseases. For example, data describing the current distribution of myrtle rust (*Austropuccinia psidii*) that affects some eucalypt species could be loaded into the ALA. A preliminary Maxent analysis of the species distribution, similar to that described by Berthon et al. (2018) could be carried out within the ALA.

2.14. Integrating species and environmental data – ALA – Desirable future developments

All users interested in biodiversity and forestry around the world should have access to systems similar to the ALA. The GBIF is using the ALA as a model for other systems, and the ALA has made program code freely available to assist the development of similar systems in more than 11 countries including Brazil, Canada, France, Spain and the UK (see http://living-atlases.gbif.org/ for current details). To assist data analyses within and between countries it would be good if these systems all provided the standard global gridded soil data being developed by ISRIC (see Section 2.3). Ideally, the ability to interpolate both climatic and soil data to actual locations would also be desirable in the longer term. These biodiversity databases should also provide links to systems like the BCCVL to facilitate analyses of different climatic change scenarios.

3. Discussion

A search on Google Scholar indicates that the uptake of SDM modelling techniques generally has been dramatic in recent years with many hundreds of studies completed in a wide range of terrestrial and marine environments (see Fig. 1). A number of key SDM-related issues have been identified including the use of presence only or presence/(pseudo-)absence data, errors and uncertainties associated with SDMs (Gould et al., 2014) and variable selection (Porfirio et al., 2014). These issues, and other generic SDM considerations, are all examined in the three SDM/ENM/HSM books (Franklin, 2009, Peterson et al., 2011, Guisan et al., 2017).

The progress relevant to SDM applications for both native and plantation forests has also been remarkable (see Table 2). However, the use of SDM analyses for forestry climate change studies are not without their particular limitations (see Table 1). One of the most important limitations, not mentioned in Table 1, is their inability to account for the impacts of atmospheric as well as climatic change. Studies of both plantation and native stands of eucalypts grown under raised carbon dioxide conditions are providing insights into these impacts (see, for example, Ellsworth et al., 2017), which can be incorporated into process-based models. Though SDM and process-based models are sometimes seen as alternatives, they can be complementary. A process-based model can be run for a small number of locations to complement the results of a broader SDM analysis.

At present SDM models are the only practical way to consider the impacts of climate change on large numbers of species at many locations. Though the limitations considered in Table 1 should not preclude their use, they should be used with due caution. Predicting likely changes is particularly difficult for species that have effective dispersal means. Accordingly, it is recommended that emphasis should be placed on using SDMs to identify the potentially most vulnerable species and areas under climate change which should be carefully monitored (see, for example, the 657 maps for eucalypt species produced by González-Orozco et al., 2016). Identifying potentially vulnerable sites under climate change could be carried out for both native forests and plantations. Comparing these predictions against observations in coming decades would allow the SDM models to be validated and refined. At present, evidence is contradictory with some studies reporting rapid shifts in tree species which can be attributed to climate change (Kelly and Goulden, 2008), and others a lack of response (Zhu et al., 2012).

The progress with SDM tools and data since 1991 has been impressive, so it is appropriate to set challenging future goals (Table 2). Estimating climatic and soil conditions at actual occurrence locations, rather than taking estimates from the nearest grid cell would be demanding, but should be an achievable goal in the foreseeable future as the interpolation relationships already exist. Incorporating the effects of local topography on factors such as insolation, frost and water balance at particular sites will be more difficult, but should provide benefits. Collating absence data as well as presence data will also be challenging, but should be achievable at least for trees. Absence data is essential for understanding climate change impacts, so it is known if a species is now absent from areas where it was once present. It would be desirable if data from species and provenance trials could be collated in the same way that natural distributional data have been collected. It appears unlikely that a major effort will be made to collate these data, but at least the internet has made accessing relevant published data much easier. The development of ALA-like systems around the world should be inevitable, as the power of integrating SDM facilities within one

Table 2
Progress with SDM-related topics and possible future objectives.

Topic	1991	Now	Possible future objectives
Climatic data	Sparse meteorological stations for most countries	WorldClim 1 km	Estimate for actual occurrence locations
Soil data	Sparse samples	SoilGrids250m	Estimate for actual occurrence locations
Distribution data	Some occurrence lists e.g. 44 000 native eucalypt records used by Hughes et al. (1996)	ALA > 910 000 eucalypt records GBIF > 56 000 eucalypt records outside Australia	Create best possible native and introduced coverage for all tree species
Trial data	Reports accessed via libraries	Reports accessed via internet	Develop TREDAT-like database
Descriptions of species requirements	See, for example, Webb et al. (1984)	CABI (2005) Forestry Compendium or 124 SDM analyses from Dyderski et al., 2018	Develop global database using non-equilibrium assumption-based SDM descriptions
Mapping of suitable areas	Microcomputer-based climatic mapping programs	GIS & internet-based systems such as the ALA	Develop ALA-equivalent standard systems for all continents or major regions

ALA – Atlas of Living Australia.
CABI – CAB International.
GBIF – Global Biodiversity Information Facility.
GIS – Geographic information system.

system is so obvious. ALA-like systems should also become even more powerful as high resolution soil data are included. Together with facilities like the BCCVL these systems provide great tools to help assess the impacts of climate change on plantations as well as natural forests.

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